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Stethacanthid Elasmobranch Remains from the Bear Gulch Limestone (Namurian E2b) of Montana

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ABSTRACT

Four chondrichthyan species assigned to the cladodontid genus *Stethacanthus* are described from the Bear Gulch Limestone of Montana. Specimens are referred to *Stethacanthus* cf. *S. altonensis* and *S. cf. S. productus*. Two other species are too immature to assign with certainty to known stethacanthid spine species. The histology and morphology of three isolated cladodont tooth types is described, one of which is referred to *Cladodus robustus*. The species of Stethacanthidae are distinguishable on the shapes and proportions of pal-

atoquadrate and mandible, numbers of tooth families and pectoral prearticular basals, morphology of the pelvic girdle and areas of squamation. Comparison with other Bear Gulch stethacanthids strongly suggests that the presence of specialized cranial and first dorsal fin squamation, with the presence of the first dorsal fin and spine, are secondary sexual characters of mature males. *Cladoseleache* is indicated as the sister group of the Stethacanthidae, with the "Symmoriidae" being the sister group of *Stethacanthus altonensis*.

INTRODUCTION

The Upper Mississippian marine Bear Gulch limestone member of the Heath Formation has yielded approximately seven species of cladodont elasmobranchs referable to the family Stethacanthidae (Lund, 1974). Several of these have been found in sufficient abundance or completeness to allow adequate holomorphic diagnosis and description (Lund, 1974, 1984, 1985, in press). These

taxa have also provided excellent data on the relative values of the spines and other morphological parameters for gross diagnostic differentiation, and have particularly demonstrated that striking sexual dimorphism within the family may pose insurmountable difficulties in the recognition and diagnosis of incomplete or inadequately represented forms. Causing particular difficulty are the

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observations that only males may possess the characteristic first dorsal spines and fins, and only at sexual maturity (Lund, 1984; *Falcatus falcatus*, Lund, 1985; probably *Stethacanthus altonensis*, Lund, 1974 and below; *S. cf. S. productus*, below). In one other, "*Physonemus*" *attenuatus* (Lund, in press) there is considerable change of form of the first dorsal spine and braincase with growth, but females are not known for this species. Additionally, marked differences occur in the abundances of males versus females in all groups with striking sexual dimorphism (Ghiselin, 1974; also see Lund, 1982). Further, sexually dimorphic living elasmobranchs of different sexes may occupy different ranges at different times (Branstetter, 1981), suggesting that there may be difficulties in locating or recognizing fossil chondrichthyan of the sex opposite to that of the type specimen. Following from this information, the purported absence of claspers in *Cladoselache*, for instance, may more reasonably be attributed to either an absence of mature males at the localities searched or an inability to recognize males than to the remote possibility that this rather specialized chondrichthyan lacked claspers (Harris, 1938, 1951; Zangerl, 1981; Rosen et al., 1981).

This report will describe Bear Gulch shark specimens that are too rare or too incomplete to assign with certainty to a previously named species, but that are critical to understanding the morphological differences between species within the Bear Gulch *Stethacanthidae*.

ABBREVIATIONS: Specimens have been deposited either with the Section of Vertebrate Fossils, Carnegie Museum of Natural History, Pittsburgh, Pa. (CM), or with the Geologic Museum of the University of Montana, Missoula, Montana (MV).

DESCRIPTIONS

Stethacanthus cf. S. productus

Newberry, 1897

Figures 1, 2, 7F

PREVIOUS REFERENCES: *Stethacanthus altonensis* Lund, 1974, fig. 10, CM 23654. *Stethacanthus cf. S. productus* Lund, 1984.

REFERRED SPECIMENS: CM 23654, whole, immature, disturbed specimen; CM 35695, palatoquadrate; CM 37669, palatoquadrate; MV 6160, pectoral and pelvic girdles.

The specimen CM 23654 was originally referred to as a female *S. altonensis* (Lund, 1974). The spine of the specimen is immature and therefore proximally incomplete. The apical angle of the spine is approximately 24° and the structure of the spine suggests that the apex was a posterodorsal continuation of the base (fig. 2D). The apical angle of the spine of *S. altonensis* is 34° and the apex projects dorsally in relation to the base (Newberry, 1889, 1897; Lund, 1974). No traces of dorsal fin elements are preserved.

In dorsal view, the neurocranium is proportioned essentially as in *S. altonensis*, but with broader supraorbital crests. The palatoquadrate has grooves for 6–8 tooth families, as in *S. altonensis*, but the palatine portion is dorsally concave and the postorbital expansion is rounded posterodorsally. There is no visible extension of the palatoquadrate anterior to the mesially inturned ethmoid process. A quadrate shelf is absent, and the quadrate condyle extends below the level of the tooth row. Meckel's cartilage is unknown, but clearly had relatively few tooth families and an anteriorly placed coronoid process. The hyomandibula is stout and held in close association with the palatoquadrate, particularly near the quadrate condyle (fig. 1). "Stemmatodus"-type branchial denticles are evident.

The pectoral fin is supported by 12 or 13 prearticular basals, and eight radials are supported on the metapterygial plate. The metapterygial axis is poorly preserved. The pelvic girdles are triangular, with six conspicuous diazonal foramina, and a very small metapterygial plate. Each girdle supports at least 12 single-jointed radials. Clasper elements are unknown.

The second dorsal fin consists of a minimum of 19 separate but closely spaced, one-jointed radials, the distal segments of which are quite elongate. The posterior portion of the fin is followed by a thin triangular plate, but it cannot be determined whether this plate supported fin radials as in *Falcatus falcatus* (Lund, 1985). The caudal fin, as illustrated in Lund (1974), is heterocercal, and of relatively high angle, with separate neural arches and spines and discrete dorsal and ventral lobes. Precaudal neural arches are paired, long and thin, and lack median neural spines.

Squamation is unknown, although loose

denticles are present in MV 6160. Although no specimen is complete, and therefore no accurate length measurements can be made, the length of CM 23654 approaches 1 m, and the palatoquadrate is 11.6 cm in length. The palatoquadrate CM 37669 is 24.5 cm long, suggesting a total length of around 2 m for an intact individual. *S. cf. S. productus* is thus significantly larger than *S. altonensis*, and the largest known vertebrate in the Bear Gulch Limestone. This size differential is reflected in the sizes of known spines of the two species (Newberry, 1889, 1897).

Stethacanthus cf. S. productus differs from *S. altonensis* in the shape of the pterygoid portion of the palatoquadrate, the higher number of prearticular basals of the pectoral fin, the morphology of the pelvic girdle and fin, and in the relative length of the radials of the second dorsal fin, as well as in the shape and size of the first dorsal fin spine. The two species are significantly similar, however, in braincase shape, general plan of the pectoral fin, and particularly in lacking a large metapterygial plate of the pelvic fin. The immaturity of the first dorsal fin spine of CM 23654, a moderately large specimen, is striking, suggesting that as in *Falcatus falcatus* (Lund, 1985) the first dorsal fin spine is a secondary sexual character present only in mature (probably male) individuals.

Stethacanthus cf. S. altonensis

Figures 3 and 4

REFERRED SPECIMEN: CM 37680.

This specimen consists of jaws, eye pigments, branchial and pectoral skeleton, vertebral axis with 54 segments, dislocated braincase, and digestive tract contents. Calcification of the neurocranium of the 10.8 cm fossil is incomplete anteriorly. The specimen is referred to *S. altonensis* on the basis of the following: palatoquadrate has an angular slope of the dorsal margin of the palatine portion to the pterygoid portion; the posterior margin of the palatoquadrate is almost squared off relative to the posterodorsal outline; the posterior margin has a tall, narrow quadrate shelf (fig. 3; Lund, 1974) as well as a pectoral fin supported by three anterior unjointed radials and seven single-jointed radials plus the metapterygial plate (fig. 4). The metapterygial plate supports eight radials.

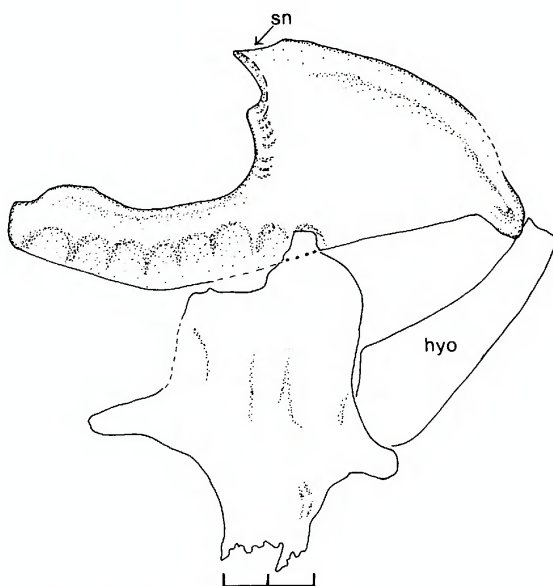


FIG. 1. *Stethacanthus cf. S. productus* Newberry, 1897. CM 23654. Neurocranium, palatoquadrate, and hyomandibular, mesial view. Scale in cm; hyo, hyomandibular; sn, spiracular notch.

The contents of the digestive tract consist of an entire, although fragmented, conodontochordate (Melton and Scott, 1973; Scott, 1973).

The neurocranium has broad supraorbital crests and a very strong postorbital arcade. The otic region is broad and flat ventrally, narrower and rounded dorsally, with prominent ridges for anterior and posterior vertical semicircular canals. Serial supraorbital foramina for Ramus Ophthalmicus Superficialis fibers supplying the supraorbital lateral-line canals are present dorsally, and a median basal foramen, probably for the hypophysis and internal carotid arteries (Jarvik, 1977), is present midventrally.

The mandible has a high coronoid process slightly posterior to its midpoint, and indistinct grooves for seven tooth families. Teeth in both upper and lower jaws are large and five-cusped, with the medial and most lateral cusps strongly fluted. The teeth are predominantly of orthodentine in visual inspection, osteodentine being absent from the pulp cavities of the cusps. A variety of branchial denticles is present, including those of the "Stemmatodus" type.

The axial skeleton contains 54 paired neu-

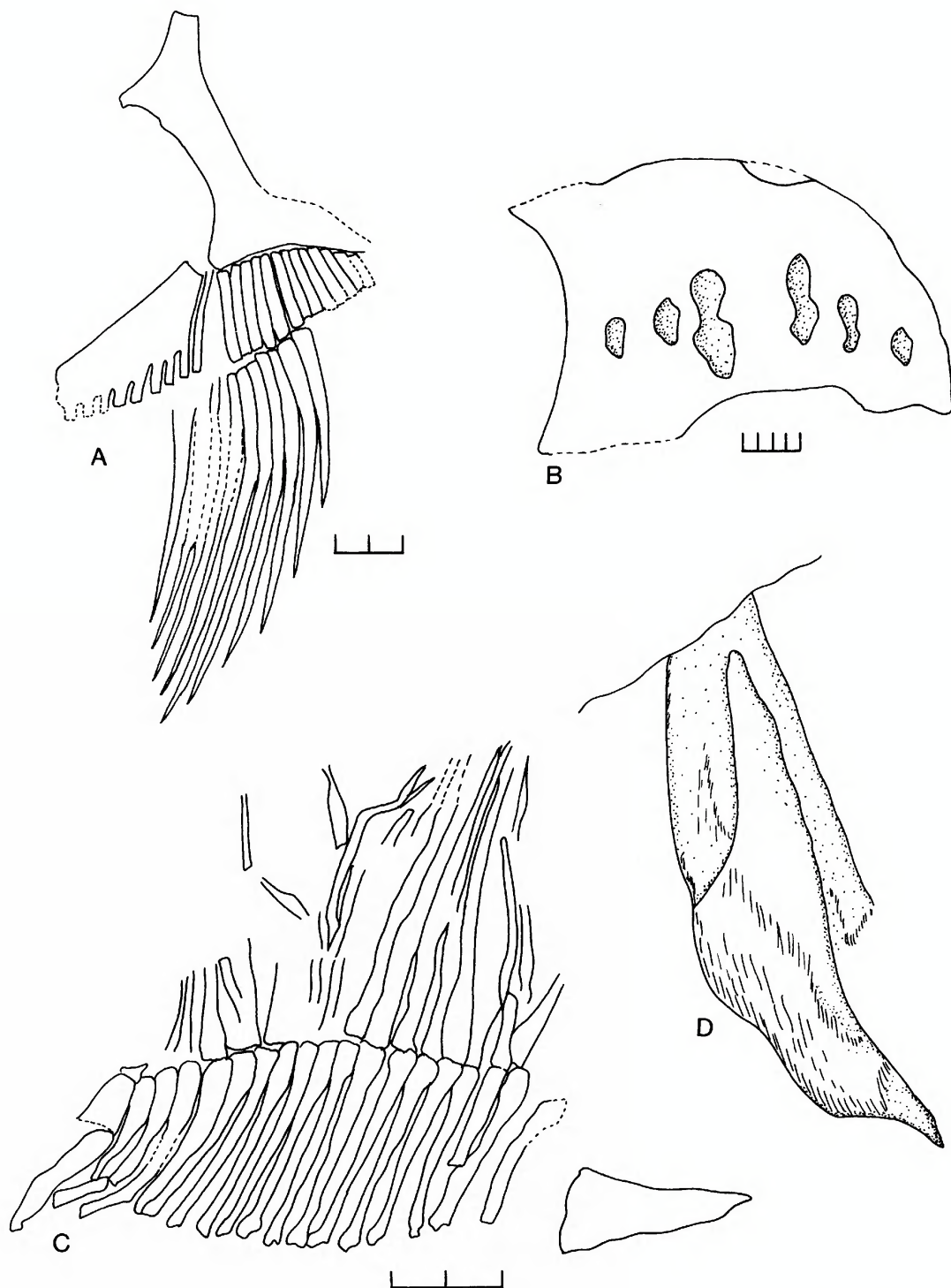


FIG. 2. *Stethacanthus* cf. *S. productus* Newberry, 1897. CM 23654. (A) pectoral fin; (B) pelvic girdle; (C) second dorsal fin; (D) first dorsal spine, anterior to the right. A–C, scale in cm; D, maximum width 12 mm.

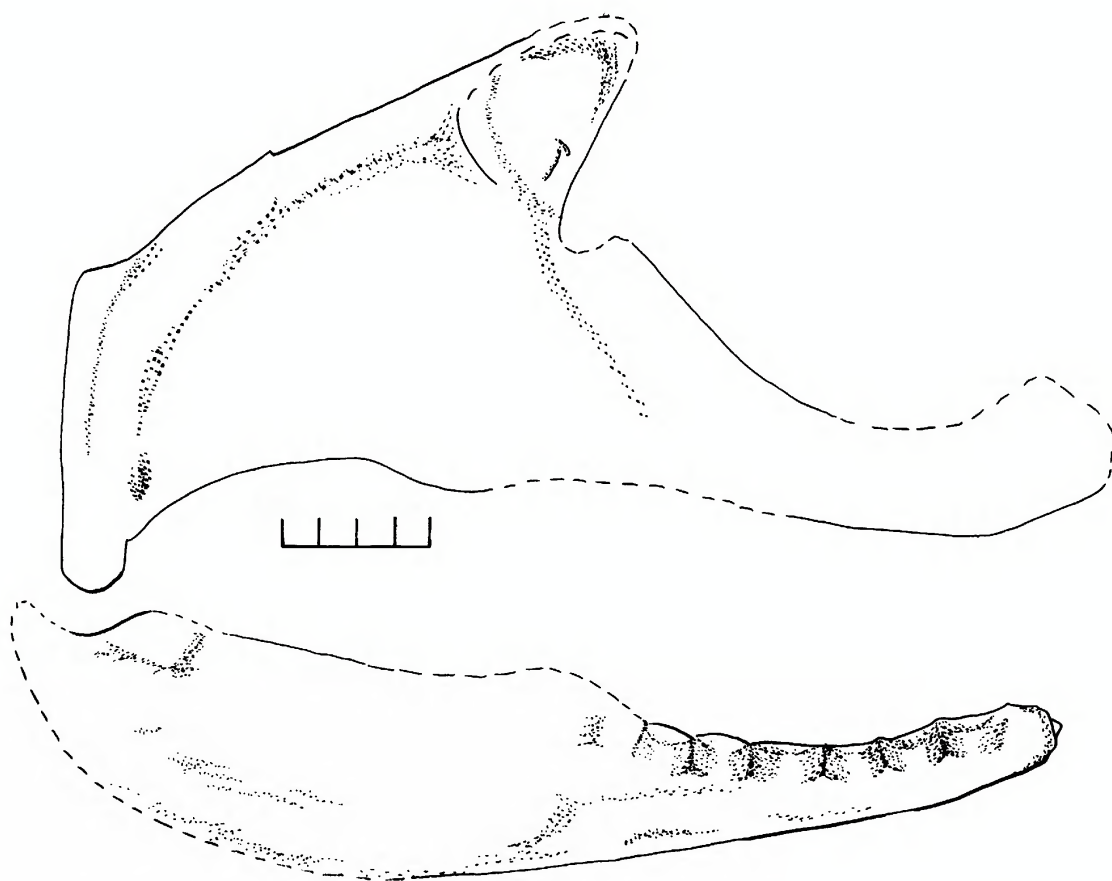


FIG. 3. *Stethacanthus* cf. *S. altonensis* (St. John and Worthen, 1875). CM 37680, palatoquadrate and mandible. Scale in mm.

ral arches fused in the dorsal midline and bearing slight neural processes dorsally. Dorsal root foramina are included in all visible neural arches, while ventral root foramina appear to be intersegmental. There are no traces of intercalaries, arcualia, or basapophyses. The axial skeleton is downfaulted into the matrix at a region of marked change in the form of the neurals; they become considerably narrower, more closely spaced, more posteriorly inclined, and more elongate than the anterior elements. This transition marks the proximity of the caudal portion of the axis (fig. 4B).

A portion of the anterior trunk lateral-line canal is present as well as melanin-derived traces of former skin pigmentation. The lateral-line canal is supported by highly modified scales in the form of half rings, which

also characterize other Bear Gulch stethacanthids (Lund, 1984, 1985, in press). Other squamation is absent. Further, there is no indication of specialized cranial squamation of the sort that characterizes known adult males of the stethacanthids within (Lund, 1984, 1985, in press) or outside of the Bear Gulch Limestone (Zangerl, 1981).

Stethacanthus sp. 1

Figure 5

REFERRED SPECIMENS: CM 35456, CM 35487, two partial specimens of approximately 360 mm total length (260 mm length to the posterior pelvic margin) and 162 mm length to the posterior pelvic margin, respectively.

The palatoquadrate has a high, stout ethmoid process with a slight forwardly pro-

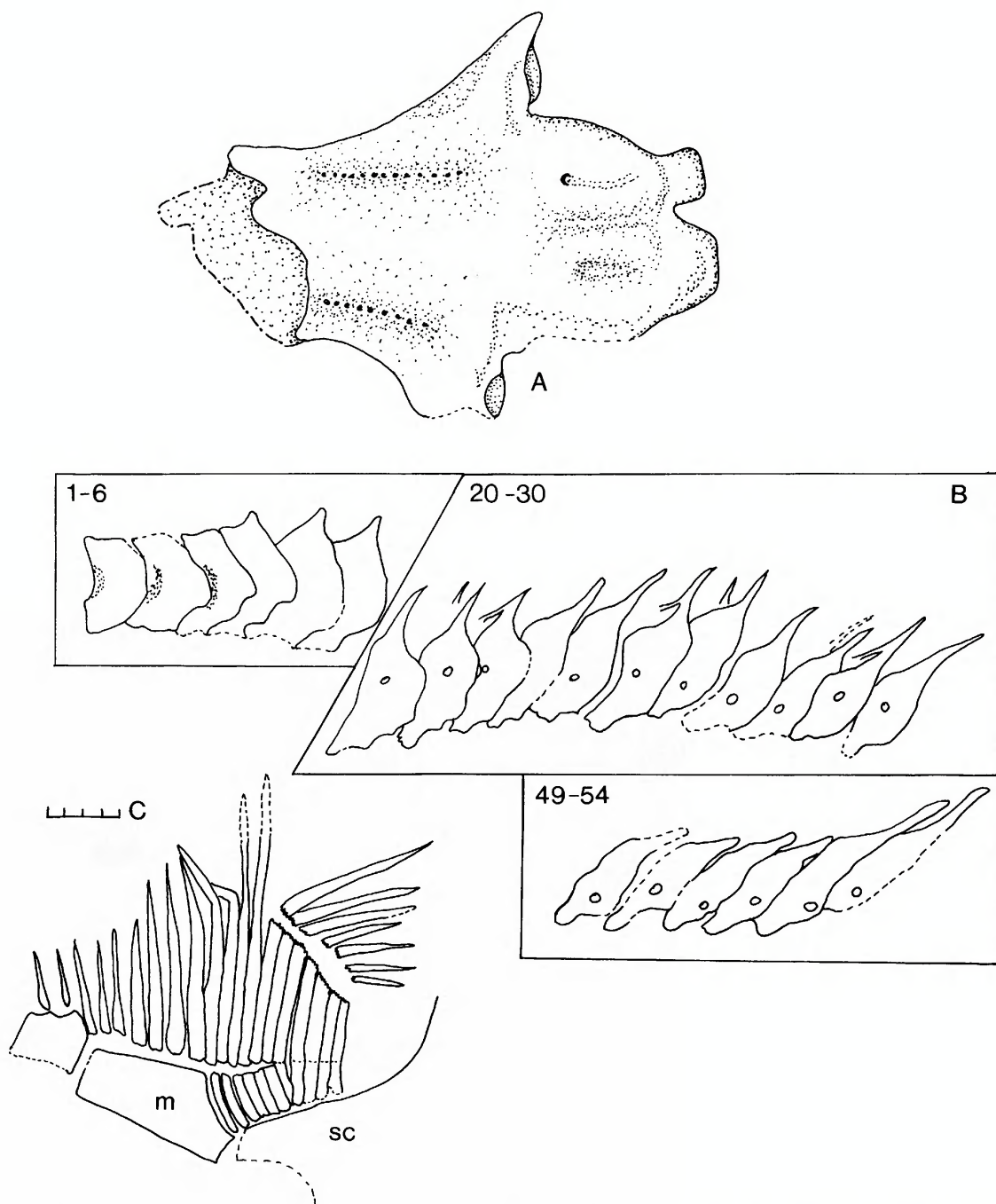


FIG. 4. *Stethacanthus* cf. *S. altonensis* (St. John and Worthen, 1875). CM 37680. (A) neurocranium; (B) neural elements of segments 1-6, 20-30, 49-54; (C) pectoral fin. m, metapterygium; sc, scapulocoracoid. Scale in mm.

jecting absymphyseal process. The palatine region is almost straight, its dorsal margin curving only slightly to meet the prominent

pterygoid region. The posterodorsal margin of the pterygoid region descends in a straight line to meet the prominent short vertical

quadrate shelf. The quadrate condyle is at the level of the tooth row. There are grooves for 10–11 tooth families. The tooth-bearing portion of the mandible is 73 percent of its total length, contains grooves for 11 tooth families, and the coronoid process is not prominent. The mandible is moderately deep throughout. Teeth are uniformly small and strongly fluted.

The pectoral fin contains seven or eight prearticular basals, a basal plate supporting eight radials, and three visible axial elements with two radials per axial. The coracoid is directed ventrally, while the scapula has a short anterodorsal extension and lacks a posterodorsal extension. The pelvic girdles, from either juveniles or females, each consists of an elongate plate with calcified parallel ridges and a series of four diazonal foramina medially. Posteriorly, the small metapterygium supports the last three of fifteen unjointed, well-spaced radials. The two girdles are in extensive contact in the midline.

The dorsal fins are poorly preserved. The 39 precaudal neural arches are paired, slender, and only the anterior arches have included dorsal root foramina. Other details are obscure. The caudal fin is low-angle heterocercal, but has a strong series of radials supporting the ventral lobe.

Squamation consists of strong belts of enlarged ventrolateral flank denticles between the pectoral and pelvic girdles. There is some evidence for finer, pointed denticles higher on the flanks.

The two specimens are united on the common possession of a unique pelvic girdle, as well as the common morphologies of the palatoquadrate and mandible. In neither specimen is there any indication of calcification of the neurocranium.

Stethacanthus sp. 2

Figure 6

REFERRED SPECIMEN: CM 37671, small dorsoventrally preserved individual (86 mm to the posterior pelvic margin) lacking caudal region.

This specimen is quite incomplete, lacking a braincase, dorsal fins, calcified axial skeleton and caudal fin, as well as a complete palatoquadrate. The combination of char-

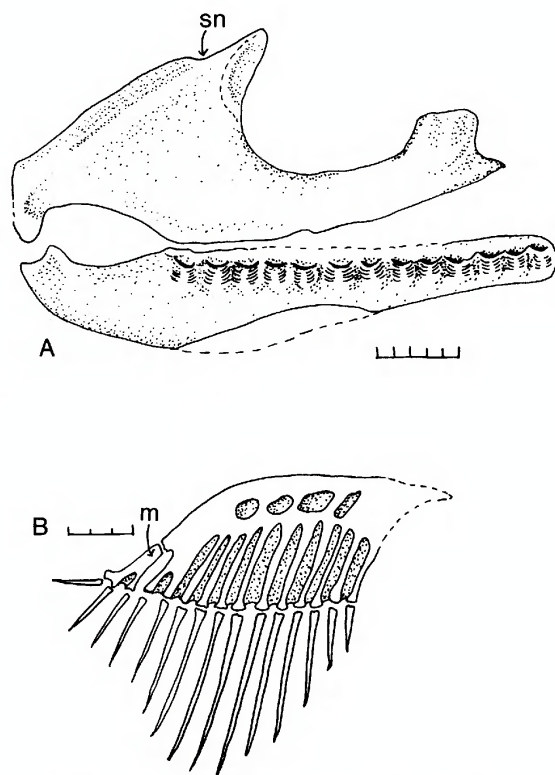


FIG. 5. *Stethacanthus* sp. 1. CM 35487. (A) palatoquadrate and mandible; (B) pelvic fin and girdle. m, metapterygium; sn, spiracular notch. Scale in mm.

acters of palatoquadrate, mandible, and pelvic girdles is unique in the fauna.

The palatine portion of the palatoquadrate is slender and dorsally concave, and there are grooves for 11 tooth families. The tooth-bearing portion of the mandible is 72 percent of its length and contains grooves for 11 tooth families; the coronoid process is relatively prominent, with the articular facet located below the level of the highest part of the tooth row. The basibranchial skeleton is indicated by encrustations of tooth aggregations, and there are sparse, long "Styptobasis"-type teeth on the ceratohyal as well as on the ceratobranchials. Two long, slender basibranchial plates are indicated. Hypobranchials apparently are short, the anterior three directed forward while the fourth is transversely oriented. Correspondence between tooth aggregations and underlying branchial elements is not assured, however (Nelson, 1970).

Prearticular basals are missing from the

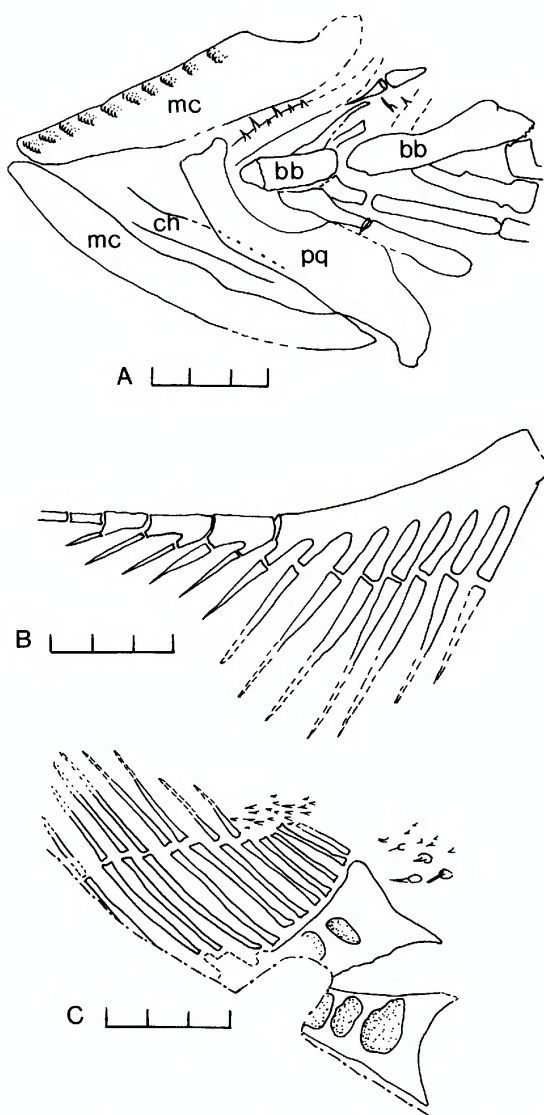


FIG. 6. *Stethacanthus* sp. 2. CM 37671. (A) visceral skeleton, dorsal view; (B) pectoral fin; (C) pelvic fins, girdles and lateral denticles. Scale in mm.

pectoral fin, but the narrow metapterygial plate supported eight unjointed radials. Five axial elements are visible, the first two supporting two radials each, the following one supporting one radial, and the remaining basals lacking radials. The pelvic girdles are triangular plates, lacking evidence for a prominent metapterygium and supporting a minimum of 12 slender, well-spaced one-jointed radials. Several large diazonal foramina or uncalcified areas occupy the center of

each pelvic plate. There is a continuous fine shagreen of conical denticles, enlarged in a belt along the ventrolateral flank between pectoral and pelvic girdles and onto the anterior edge of the pelvic fin. Lateral-line ring scales are present.

Stethacanthus sp. 2 resembles *Stethacanthus* cf. *S. productus* in the shape and proportions of the pelvic girdles, but differs from it in the proportions of the jaws, and the numbers of tooth grooves. *Stethacanthus* sp. 2 resembles *Stethacanthus* sp. 1 in the strong ventrolateral denticle belts, but the two differ in other available characters including the prominence of other squamation.

TEETH

Stethacanthus sp.

Figures 8A–D, 9, 10A–E

REFERRED SPECIMENS: CM 35458, six teeth of one disrupted tooth family, and CM 35459, seven teeth in one tooth family in articulation, both specimens with either one or two intermediate cusps round in frontal section and both specimens found in immediate proximity to each other; CM 37524, 41063, 41064, 81-63026, isolated teeth.

There are no specimens of either *S. productus* or *S. altonensis* with sufficient numbers of fully exposed teeth to permit characterization of species differences. These teeth conform to the visible teeth of *S. altonensis* (Lund, 1974). The single-layered enameloid of all large cusps is arranged superficially into fine vertical fluting, with the fluting of distal and proximal cusps somewhat sparser than that of the central cusp. All teeth have relatively prominent paired ventrolabial and buccolingual tubercles and rounded lingual plate margins (fig. 8A–D). Nutrient foramina are abundant along the lingual margin of the base, with the largest vascular canals tributary to the principal cusps and large vascular canals also located lingual to the bases of the tubercles.

Transverse thin sections were taken of a series of seven articulated teeth (CM 35459; figs. 9, 10A–C), and longitudinal sections were prepared of another tooth (CM 41064; fig. 10D, E). In section, the enameloid is single layered and isotropic, lacking obvious birefringence, indicating a very fine foliate tex-

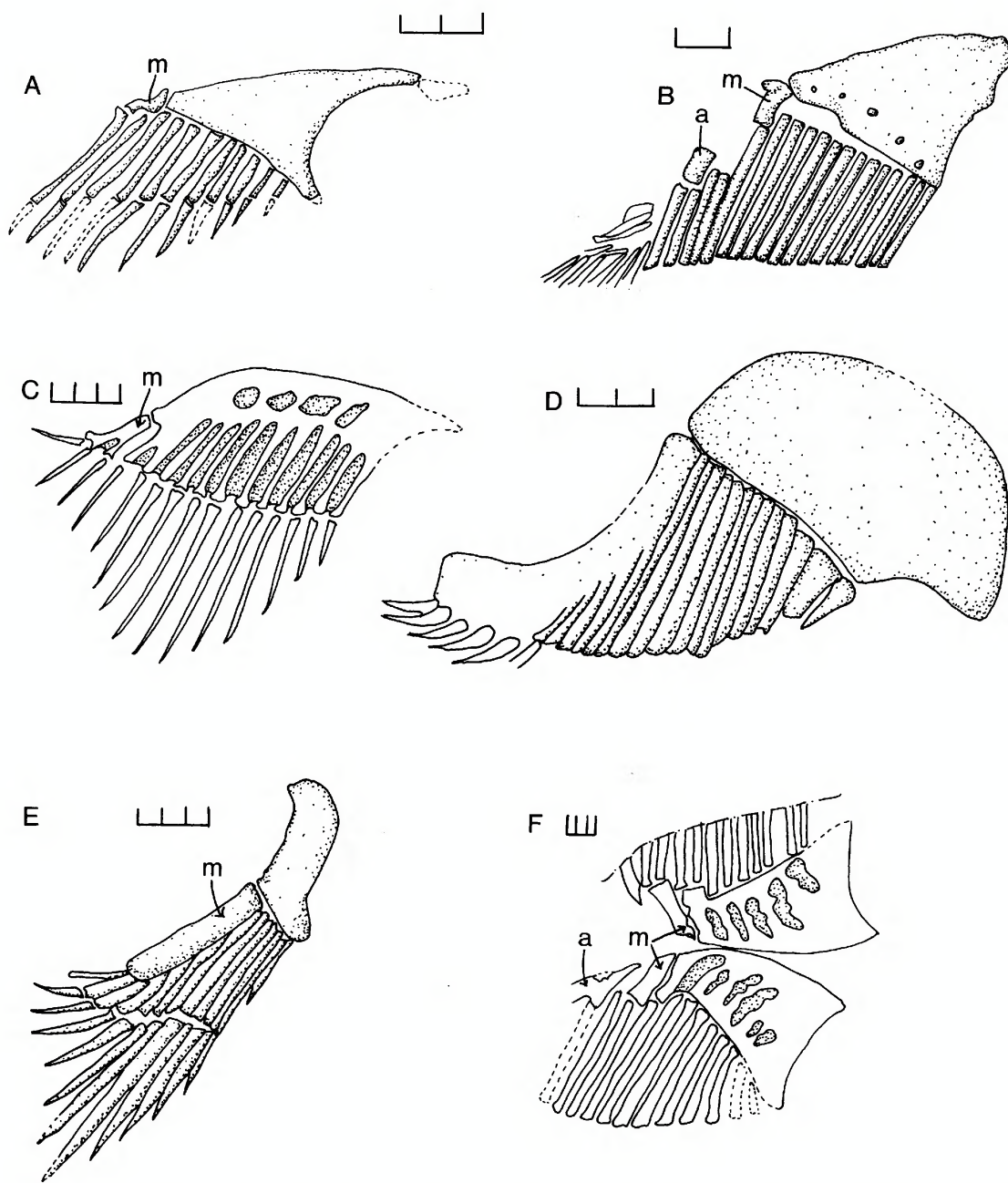


FIG. 7. Pelvic girdles of Stethacanthidae. (A) *Falcatus falcatus*, MV 5386, female; (B) *Stethacanthus altonensis*, MV 2830, male; (C) *Stethacanthus* sp. 1, CM 35487, juvenile; (D) "*Cobelodus*" *aculeatus*, from Zangerl and Case, 1976, fig. 246; (E) *Orestiacanthus fergusi* (Lund, 1984), CM 37525, female; (F) *Stethacanthus* cf. *S. productus*, MV 6160, probable male. A, C, E, F, scales in mm; B, D, scales in cm. a, axial element; m, metapterygium.

ture (durodentine, Schmidt and Keil, 1971). The superficial fluting pattern is not reflected in the topography of the dentinoenameloid

junction. The enameloid layer is underlain with a thick orthodentine mantle, characterized by parallel Tomes' processes perpendic-

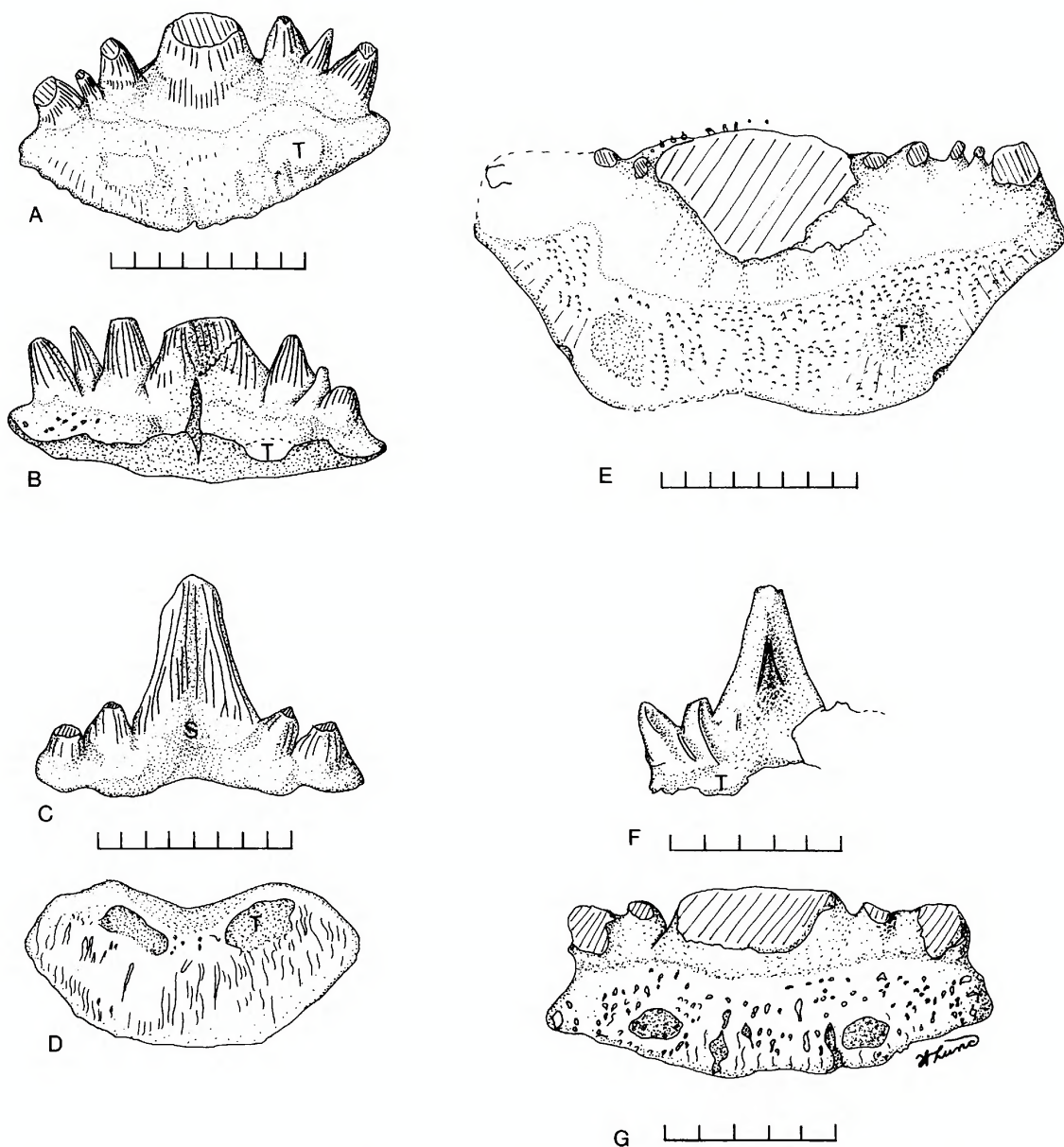


FIG. 8. *Stethacanthus* sp., CM 41063, tooth in oral (A) and labial (B) views. *Stethacanthus* sp., CM 37524, tooth in labial (C) and aboral (D) views. (E) *Cladodus robustus*, 82-72304B, basal plate in oral view. (F) *Cladodus* sp., CM 37506, partial tooth in labial view. (G) *Cladodus* sp., CM 37507, tooth in oral view. Abbreviations: S, lingual sulcus; T, tubercle. Scales in mm.

ular to the enameloid boundary. The orthodentine shows no circumferential banding under polarized light. There is an abrupt change from orthodentine to the osteodentine core, which continues vertically into the bases of the teeth (fig. 10A, D). Peritubular

dentine can be seen to line some vascular canals. There are no significant differences in coronal tissues among the articulated teeth of the radially sectioned tooth family.

Tissues of the lingual plate and ventrolabial tubercle differ from osteodentine in both

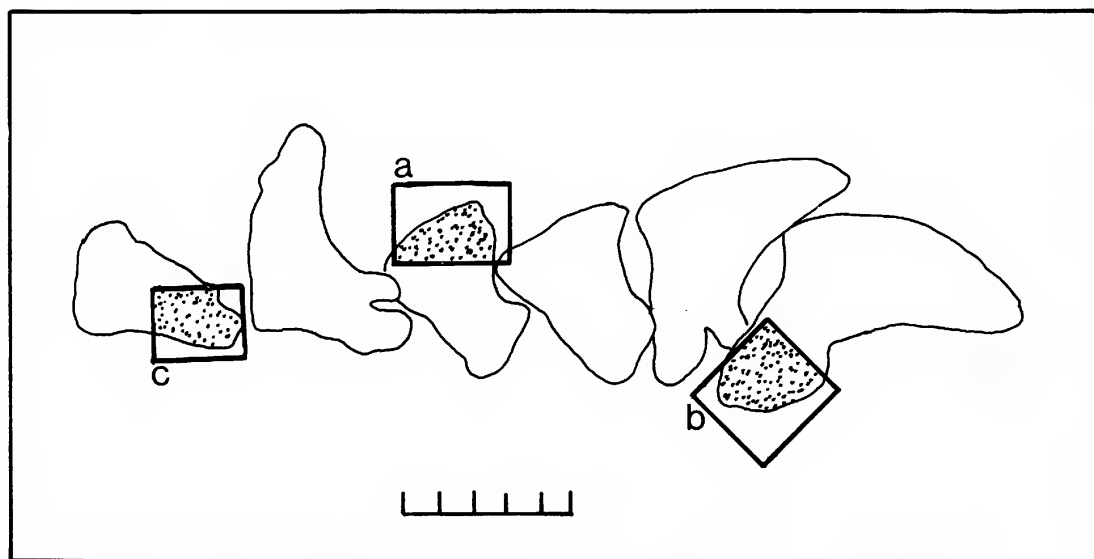


FIG. 9. *Stethacanthus* sp., CM 35459, successional tooth family in radial section. Letters correspond to illustrations in figure 10. Scale in mm.

plain and polarized light; the tissues are more darkly stained, have differing optical qualities, and lack Tomes' processes. The tissue of the lingual plate is acellular bone of the tooth pedestal, as is found in the bases of some Recent Selachii (Reif, 1979b; Moss, 1970). Two features characterize the bases of the less mature teeth of CM 35459: dorsolingually-ventrolabially arching mineralization of Sharpey's fibers (fibers of the periodontal ligament), and a similarly oriented regular set of vascular canals connected in three dimensions by rectangular cross canals (fig. 10B, C). In the more mature teeth of the specimen, the vascular canals have undergone significant diminution, Sharpey's fiber pathways no longer contact the walls of the vascular canals, and peritubular dentine is visible as a lining of some of the canals (fig. 10C). Sections of cladodont tooth bases from the Burlington Limestone of Iowa (CM 26302) reveal the same pattern of Sharpey's fibers with a somewhat different vascular pattern superimposed, and significant peritubular dentine deposition. Radial sections of the lingual plates of teeth of *Orthacanthus texensis* (CM B6/1937) show the same pattern. Neither the Burlington Limestone cladodont teeth nor those of *Orthacanthus* have enameloid.

Cladodus robustus
Newberry and Worthen, 1866
Figure 8E

REFERRED SPECIMENS: CM 41090, 82-72304, isolated teeth.

Two teeth are referred to *Cladodus robustus* (Newberry and Worthen, 1866). They are characterized by having many small intermediate cusps and relatively small proximal and distal cusps by comparison to the robust central cusp, by slightly concave proximo- and distolingual margins of the lingual plate, and by the presence of many fine denticulations along the base of the labial margin of the crown. Intermediate cusps are variably angular in frontal section and their long axes and positions are irregularly arranged upon the tooth base. In the largest tooth, CM 41090, five intermediate cusps are present to the right, and four to the left of the central cusp in a cusp row length of 27.2 mm. The cusp row length is 1.9–1.97 times the maximum width of the lingual plate.

Cladodus robustus teeth are the only teeth in the fauna large enough to have fit into the tooth grooves of the palatoquadrate of *Stethacanthus productus* (CM 37669, above). There are no associations between the teeth and the palatoquadrate, however.

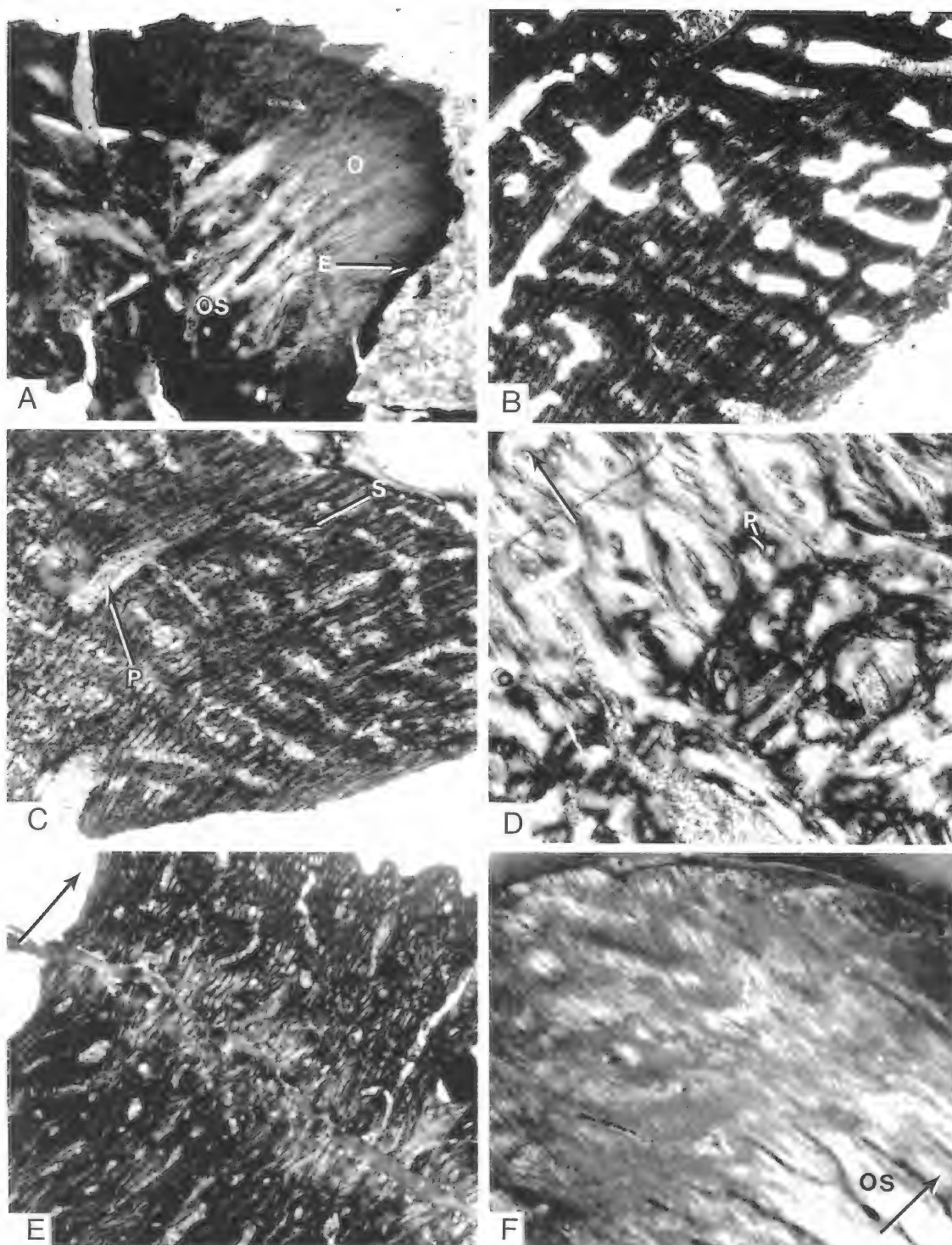


FIG. 10. *Stethacanthus* sp., CM 35459: (A) central cusp, tangential section. (B) lingual plate, early tooth. (C) lingual plate, more mature tooth. *Stethacanthus* sp., CM 41064: (D) osteodentine base of central cusp, longitudinal section. (E) bone, lingual plate, longitudinal section. (F) *Cladodus* sp., CM

Cladodont indeterminate

Figure 8F, G

REFERRED SPECIMENS: CM 37506, 37507, 37675.

A form of cladodont tooth that does not conform to those of the known Stethacanthidae is known only from three isolated specimens. The proximal and distal margins of each cusp are drawn into enameloid blades, the central cusp is compressed linguolabially, there is only one, stout intermediate cusp between central and extreme cusps, and the labial surface of each cusp bears one or two short, prominent, sometimes basally bifurcating enameloid ridges that often extend to the crown-base border on the intermediate cusps. The tooth bases extend lingually beyond the labial margins of the teeth, and the lingual margin of the base roughly parallels the tooth row. There are numerous nutrient foramina in several rows dorsally, the largest of which are concentrated near the lingual margins. Two tubercles are located ventrally along the labial margin, directly under the intermediate cusps. The height of the central cusp differs by two times in proportion to the remaining cusps among the three teeth. This difference cannot be attributed strictly to wear.

DISCUSSION

SYSTEMATIC CHARACTERS: The shapes and proportions of the palatoquadrate and mandible remain constant within each of the Bear Gulch stethacanthid species described above or cited, across a significant span of growth. Additionally, numbers of tooth families and fin radials are relatively invariant within each species. This relative constancy of form aids in ready identification of the less well represented specimens described above. "Stemmatodus" and "Styptobasis" type denticles, contrary to the assertions of Zangerl and Case (1976), are not diagnostic of a single taxon but are found on many, if not all, Bear Gulch Stethacanthidae. While the form of the scap-

ulocoracoid and its processes might prove to be of systematic significance, preservational difficulties limit the usefulness of these characters. Axial elements of the pectoral fin are also rarely well preserved.

The form of the pelvic girdle and fin, while relatively constant within species, is the most variable interspecies character in the Bear Gulch stethacanthids. Pelvic girdles fall into two broad types. The first, and almost undoubtedly primitive (Rosen et al., 1981), bears virtually the entire pelvic fin, with only the terminal radials being supported by a very small, outturned metapterygial element. Included in this category are all the specimens described above as well as *Falcatus falcatus* (Lund, 1985) and *S. altonensis* (fig. 7). The second type (Lund, 1984, in press) consists of species with a prominent metapterygial plate (fig. 7E).

Squamation varies from sparse but total with specialized areas in males while absent in females (Lund, 1984), to present only in specialized areas of males such as the dorsal surface of the head and first dorsal spine (Lund, 1974; Zangerl, 1981). Only in *Stethacanthus* sp. 1 and sp. 2 (above) is there evidence that some specialized squamation may be present in juveniles or females. A complete, unspecialized squamation, the primitive condition for Chondrichthyes, is unknown among the Stethacanthidae. Squamation, however, is uncertain or unknown in many species and differs between the sexes where known. It has limited utility as a supraspecific character at this time.

The axial skeleton, where known, provides useful information on the presence, numbers, and forms of the elements; the locations of foramina; fusions across the midline; and the form of the caudal skeleton. Numbers of pre-caudal segments seem to differ between all species and only one specimen, *S. cf. S. altonensis* (above) shows fusion of neural arches across the midline. In no case are separate neural spines known of the kind attributed

←

26302, Burlington Ls., lingual plate, radial section. All sections with crossed polars. See figure 8 for scale. Abbreviations: E, enameloid; O, orthodontine; OS, osteodontine; P, peritubular dentine; S, Sharpey's fibers. Shaded arrows indicate oral direction.

to *S. altonensis* by Zangerl (1981). Only the form of the caudal fin, whether heterocercal (primitive) or homocercal (derived; Lund, 1985, in press), is of use in supraspecific analysis because of disparities in preservation among the available specimens.

The morphology of the first dorsal fin-spine complex is unique to each described taxon of the Stethacanthidae, where known (Lund, 1984). Spines are known from a male *S. altonensis* (Lund, 1974), only from mature males of *Falcatus falcatus* and a new stethacanthid (Lund, 1984, 1985), and an immature spine from *S. cf. S. productus*. Only "*P.*" *attenuatus* spines show growth over a significant size range of males at differing stages of maturity (Lund, in press) and while females are unknown for this species, specialized cranial and first dorsal squamation correspond to those of other members of the family. There is absolutely no evidence to support Zangerl's (1981) contention that the Field Museum's *S. altonensis* (FMNH PF 2207) is a female. It cannot be established at this time how prevalent among the Stethacanthidae this form of sexual dimorphism is, but it is now known for every stethacanthid for which adequate specimen numbers and both sexes are known. There is thus evidence to suggest that the first dorsal fin and spine, with specialized cranial and first dorsal squamation, occurs only in sexually mature males of the Stethacanthidae.

While these are the only instances of the first dorsal spine and fin being secondary sexual characters among the known Elasmobranchii, Recent or fossil, similar phenomena involving head claspers have been reported for Recent Holocephali (Dean, 1909), *Squaloraja* (Woodward, 1886), and a chondrenchelyid (Lund, 1982); further, considerable sexual dimorphism in the form of the first dorsal fin, and spine and cranial squamation has been documented for *Echinochimaera* (Lund, 1977a). There are many stethacanthid spines remaining from the Late Devonian and Mississippian for which no holomorphs are known. The forms of these spines, however, convey no morphological information about their bearers.

RELATIONSHIPS

Analysis of the interrelationships of early elasmobranchs is hindered by a deficiency of whole, thoroughly described specimens. Any analysis, therefore, must be regarded in great part as an attempt to refine the questions that must be asked. The Bear Gulch material, however incomplete, suggests a diverse series of characters useful in determining these interrelationships.

The primitive condition of the squamation of the Chondrichthyes is taken to be that of a complete, densely packed dermal covering, as is found in *Cladoselache clarki*, *C. kepleri* (Claypole, 1893), and *Diademodus* (Harris, 1951) as well as other gnathostome classes. The absence of a complete squamation, as in stethacanthids and symmoriids (Zangerl, 1981) is a derived state. The absence (or presence of only specialized areas) of squamation in females and juveniles, as in *Stethacanthus* sp. 1 and 2 (above) is a derived state that cannot be adequately distinguished from a condition of complete absence without knowing the condition of well-preserved males. The concomitant derived state, therefore, in which specialized areas of squamation are secondary sexual characters, may be a more critical derived character than the mere absence of complete squamation in females and juveniles. There are insufficient data upon which to judge whether the two character states, in the sharks under consideration, are autapomorphous or serially derived.

Primitively, lateral-line scales are little-modified from the normal whole-body squamation and support the edges of lateral-line canals (Dean, 1894; Smith, 1937). The presence of fine ring scales supporting the lateral-line system is a derived condition known only in Stethacanthidae, Symmoriidae, and certain Holocephali (Lund, 1982; Zangerl and Case, 1976, fig. 34) among Paleozoic Chondrichthyes.

The teeth of the mandibular arch, that are replaced in linguolabial series in all known Elasmobranchii, can be considered to be primitively directly underlain by a basal ped-

estal of bone, as is the case with certain Recent Selachii (Moss, 1970; Reif, 1979b), Actinopterygii (Moy-Thomas, 1934; Kerebel et al., 1978), and Dipnoi (Kemp, 1979). Extended basal lingual platforms and imbricating tooth bases are found in teeth of *Cladodus*, *Carcharopsis*, *Orestiacanthus* (Lund, 1984), the xenacanth, and *Chlamydoselachus* (Traquair, 1888). *Orthacanthus* teeth differ from those of *Cladodus* in having strongly banded orthodentine and in lacking osteodentine in the cores of the cusps. The structure of the lingual platforms is essentially the same between the tooth types, however, and is considered a synapomorphy. Teeth of *Chlamydoselachus* sectioned in my laboratory differ strongly from cladodont teeth in having at least two-layered enameloid, highly branching Tomes' processes in the orthodentine, fiber trajectories in the bases generally parallel to the vascular pattern, in the acute angle between the cusps and the long, narrow bases, and in the nature of the overlap between successional teeth. Strong interdental ligaments connect the ventrolabial and dorsolingual tubercles; the presence of these interdental ligaments may be inferred for cladodont and xenacanth teeth as well. These data indicate that the teeth of *Chlamydoselachus* are only grossly convergent upon the cladodont-xenacanth condition. The primitive tooth crown condition, by outgroup comparison, is a single, simple cone as is found in Osteichthyes. The simplest condition known among mandibular teeth of chondrichthyans is the coronodont state, in which a distal-proximal series of subequal cusps are fused into a multicusp unit. This first-order derived condition is known for *Diademodus*, *Coronodus* (Harris, 1951), and *Squatinactis* (Lund and Zangerl, 1974). The interpretation of "Styptobasis" teeth as teeth of the mandibular arch (Zangerl and Case, 1976), while possible as a further derived state, is rendered considerably less likely by the presence of "Styptobasis" teeth lining the buccal cavity mesial to the mandibular arch in the Stethacanthidae (Lund, 1985, in press). These teeth, however, are not morphologically similar to those of the type species, *Styptobasis knigh-*

tiana Cope (1891); teeth virtually identical to those of *S. knightiana* have been found lateral to typical dentitional teeth of *Venustodus argutus* (St. John and Worthen, 1875; CM 41097). If the coronodont condition is plesiomorphous for the Elasmobranchii, the development of relatively low, subequal cusps of the tooth crown, as in *Hybocladodus* and *Protacrodus*, is a derived state. The cladodont (based on *Cladodus mirabilis* Agassiz, 1837) and xenacanth (based on "*Diplodus*" *gibbosus* Agassiz, 1837) conditions of the cusps, where principal and subsidiary cusps of different sizes are developed upon a synapomorphous base, are thus seen as alternate derived conditions of the crown. A final commonality of the crowns of cladodont and xenacanth teeth is the apparent lack of terminal membrane enameloid (Glikman, 1967; Duffin and Ward, 1983). Terminal membrane enameloid seems to be present in the dermal skeletons of the agnathans *Tremataspis schmidtii* and *Psammolepis paradoxa* (Gross, 1935, cited in Schmidt and Keil, 1971), *Astraspis desiderata* (Reif, 1979a), in ctenacanth, hybodonts, and Recent Selachii (Duffin and Ward, 1983; Schmidt and Keil, 1971), and Petalodontiformes (Lund, 1983). The enameloid of the teeth of *Stethacanthus* sp., however, is anomalous in lacking birefringence. This may be an artifact of the tangential section, of the presumably finely foliate nature of the crystal matrix, of the nature of the mineralization, or, least likely, of diagenetic changes (Schmidt and Keil, 1971). Most of the possible explanations indicate an outer tissue similar to terminal membrane enameloid in structure but not precisely homologous. While ultrastructural details of terminal membrane enameloid are for the most part unknown, the absence of this layer is herein considered to be a derived condition shared with Holocephali and Bradyodonti.

The evidence for the primitive state of dorsal fin numbers is presently equivocal both among the Chondrichthyes and in other gnathostome classes. Arguments of equal weight can be made for two fins, as in *Cladoseleache* (Harris, 1938, 1951), or a single fin as in the Xenacanthiformes (Dick, 1981),

Heteropetalus (Lund, 1977b), and the Chondrichthyaniformes (Lund, 1982). Evidence for the primitive morphology of dorsal fin endoskeletons is also equivocal. There are three possibilities: (1) that the primitive chondrichthyan dorsal fin was a membranous flap between spine and dorsum, as in Acanthodii; (2) that the fin was supported by a basal plate and radials, as in ctenacanth, hybodonts, and some euselachians; or (3) that the fin was supported by serial, segmentally arranged basidorsals and radials, as in *Cladoselache*, Xenacanthiformes, *Heteropetalus*, Chondrichthyaniformes, the second dorsal fins of stethacanthids and symmoriids, and certain euselachians (Dingerkus and DeFino, 1983). The latter condition is also shared primitively by Actinopterygii among the Osteichthyes, which would render it a synapomorphy of Chondrichthyes and Osteichthyes at the gnathostome level. There are few other synapomorphies uniting the euselachians and actinopterygians with the remaining chondrichthyans having basidorsal radial dorsal fins, evidence that while the condition may be synapomorphic among several of the Paleozoic shark groups, it is also subject to convergence and not necessarily an indicator of relationships between, for instance, the Hemiscyllidae (Dingerkus and DeFino, 1983) and the Stethacanthidae (Lund, 1984, 1985, in press). Possibility 2 occurs in a very limited suite of chondrichthyans that are also united by other synapomorphies (Duffin and Ward, 1983; Young, 1982) and cannot be considered primitive for the Chondrichthyes. There is no further objective evidence upon which to base a decision on whether possibility 1 or 3 constitutes the primitive condition, or whether the two possibilities are mutually exclusive. In either case, however, a dorsal fin supported by serial, two-jointed radials, as in Osteichthyes, is a synapomorphy at least for Stethacanthidae, *Cladoselache*, and the symmoriids. It is also critical to note that the primitive state involves no sexual dimorphism. Thus, the transformation of the first dorsal fin to a secondary sexual character in males with its loss (absence) in juveniles and females, assuming that two dorsal fins, as in *Cladoselache*, represent the primitive condition for the Elasmobranchii, is a derived

character state regardless of the morphology of the primitive condition. Further derived conditions of the first dorsal fin of Stethacanthidae involve the sagittal narrowing of the base of the fin (stenobasal dorsal fin; *Stethacanthus*), the narrowing of the body of the fin (*Orestiacanthus fergusi* Lund, 1984), and the loss of contact between the fin, modified into a rod, and the dorsum of the body (*F. falcatus*). The total absence of the first dorsal fin of "*P.*" *attenuatus* is a final derived state (as in symmoriids), but it is not presently possible to determine whether the fin actually fused with the first dorsal spine during an early growth stage, or was independently lost. Conversely, the absence of a first dorsal fin in symmoriids could be considered primitive and the *Cladoselache*-stethacanthid condition derived except for the extremely close morphological resemblances in all other derived characters of median and paired fins, suspensorium, jaws, and teeth.

The primitive condition of the dorsal spine is single, superficial, small, and thornlike, with superficial dentinal ornamentation. This condition is known from *Antarctilamna* (Young, 1982) and *Heteropetalus* (Lund, 1977). The extension of the spine into a superficially attached rod, as in the later xenacanth (Dick, 1981) is an apomorphic state. The development of a deep sagittal insertion, as in the ctenacanth and many Neoselachii (Maisey, 1981) is another apomorphic state, as is the presence of two dorsal fin spines. The sagittal enlargement of a small superficially inserted spine as in Stethacanthidae and *Cladoselache* (Harris, 1951), and the loss of dermal ornamentation, are separate derived conditions. The primitive condition for the Stethacanthidae is represented by the spine of *Stethacanthus productus*, that is posterodorsally extended, only moderately sagittally enlarged, and not present in sexually immature specimens. Intermediate derived states of the spine are seen in the spines of *S. altonensis* and *Orestiacanthus fergusi*, where the base is sagittally enlarged and the apex of the spine is oriented vertical to the long axis of the body. Differential growth of the base of the spine, producing a forwardly inclined apex, as in *F. falcatus*, is an apomorphous condition. Distinction between species with forwardly in-

clined apexes is on the basis of degree of inclination (Lund, 1984, 1985, in press). Major differences between the *F. falcatus* complex and "*P.*" *attenuatus* include an extended period of growth and the great anterior extent of the spine in the latter genus, and significant form differences between the bases of the spines. "*P.*" *attenuatus* also lacks any trace of a dorsal fin component.

As with the first dorsal fins, the presence of an anterior dorsal spine in all growth stages of both sexes is considered to be a primitive character. The loss of the spine in females and juveniles with secondary sexually correlated development in males is therefore a derived character, and shape differentiation of the spine into a highly modified structure provides a small suite of further derived states. The apparent absence of a dorsal fin spine in male symmoriids is a derived condition that may be either convergent upon the conditions seen in all known female and juvenile Stethacanthidae, or a shared derived state.

The primitive number of pectoral prearticular basals is greater than the derived tri-basal condition that characterizes the ctenacanth, hybodonts, and Neoselachii (Duffin and Ward, 1983). The number of pectoral metapterygial axials, while also not precisely known, is primitively two to three (Rosen et al., 1981), as in *Cladoselache* and *Danaea* (Bendix-Almgreen, 1975); the increased numbers and extension of metapterygial axials into an axial "whip," as in Stethacanthidae and Symmoriidae, is a synapomorphy.

The primitive state of the pelvic plate, regardless of sex, is a subtriangular, paired structure with a metapterygial axis of one to two segments; more than 75 percent of the fin radials are borne directly upon the pelvic plate. The primitive condition is found in several Osteichthyes (Rosen et al., 1981) as well as several of the Stethacanthidae and symmoriids. For the purposes of this paper, a single metapterygial element supporting only one or two radials is considered primitive. As around 12 radials supported on the pelvic plate seem to be the modal quantity, numbers significantly higher (18–21), as in *Stethacanthus* and the symmoriids, are considered derived. Broadening of the pelvic plate into a more rounded form, accompanied by

a significant increase in radial numbers, constitutes two derived character states uniquely held in common between *S. altonensis* and symmoriids. An S-curvature of the metapterygial axis laterad from the long axis of the pelvic plate also characterizes the *Stethacanthus*-symmoriid group. Male *Stethacanthus* have multisegmented metapterygial axes (Lund, 1974; fig. 7B). Male symmoriids, however, have a single, enlarged, S-shaped metapterygium rather than a series of elements, a further derived state; no metapterygial elements are described in females (Zangerl, 1981). While small diazonal foramina in the pelvic plate are characteristic and apparently primitive, the presence of large diazonal foramina in *S. productus* seems to be an autapomorphic character. Among the stethacanthids with a single metapterygial element, the lengthening or condensation of the metapterygium to support 50 to 60 percent of the fin radials is a derived condition. Two species share this character in the Stethacanthidae, "*P.*" *attenuatus*, where the female condition is unknown, and *Orestiacanthus fergusi*, in which the metapterygium of the female supports 60 percent of the fin radials, a derived condition paralleling that of ctenacanth, hybodonts, and Neoselachii. The metapterygium of male "*P.*" *attenuatus* is a triangular plate supporting 50 percent of the unjointed, dorsoventrally flattened, closely packed radials; it appears to be uniquely derived from the condition found in *F. falcatus* (fig. 7). All Euselachii and Holocephali have a prominent metapterygium (Dean, 1909; Dick, 1978), although the form of this element and its relationship to the clasper axis in males of the two subclasses suggest that the two metapterygia are not strictly homologous.

Jointed pelvic radials are considered primitive. The condition of *Stethacanthus* sp. 1 is atypical in that it appears to result from the fusion of the proximal radial segments with the girdle, as well as the apparent broad contact of the two girdles in the midline.

Zangerl (1981) maintains that the pelvic plates of the symmoriids were positioned vertically in the body wall, an assertion from Dean (1909) that the diazonal foramina and plate-radial relationships of the specimens do

not support (Bendix-Almgreen, 1975). The pelvic plates, as in other chondrichthyans except for Holocephali and Iniopterygii (Lund, 1977a; Zangerl and Case, 1973) were positioned horizontally in the ventral body wall.

Cladoselache has not been found with claspers, negative evidence that has commonly been transmuted into a definite statement of absence (Rosen et al., 1981). It should also be noted that the pelvic fins and girdles of *Cladoselache* and *Diademodus* are almost as poorly known (Harris, 1951; Bendix-Almgreen, 1975), leading Harris to suggest that claspers preceded well-defined pelvic fins and girdles. Further, Harris noted that specimens of *Cladoselache* in which the dorsal fins are well displayed do not all have a dorsal spine. Aside from the dangers of using negative evidence when claspers are known in *Diademodus*, a "uniquely primitive" chondrichthyan (Harris, 1951), there are alternative explanations for this absence that must be considered. One is that, as in some Recent Elasmobranchii, mature males and females may have occupied separate ranges for part or most of the year (Branstetter, 1981). Another, and not exclusive, possibility is that claspers of *Cladoselache* are inadequately calcified or ossified and not subject to ready preservation, either generally or depending upon the state of maturity of the specimens at death. As claspers do not commonly calcify until sexual maturity, and virtually nothing is known about the growth of *Cladoselache*, to assume that claspers are primitively absent only in *Cladoselache* among known chondrichthyans of the same clade is insupportable. It would be more parsimonious to suggest that specimens of *Cladoselache* may be displaying size and sexual dimorphism both in the absence of claspers and the irregular occurrence of dorsal spines.

An anal fin is present in Osteichthyes, Acanthodii, Euselachii, Xenacanthodii, and Chimaeriformes. The absence of an anal fin in *Cladoselache*, Stethacanthidae, and symmoriids is a synapomorphy.

It is generally accepted that a heterocercal caudal skeleton is primitive for the Elasmobranchii, and that a hemiheterocercal or homocercal condition is derived. It is also accepted, in the absence of evidence to the

contrary, that segmentally arranged calcified or ossified vertebral arcualia are primitively absent, and their presence, as in Chondrenchelyiformes (Lund, 1982), *F. falcatus*, and "*P.*" *attenuatus*, is a derived character.

Two characters displayed by the Stethacanthidae are worthy of note, although they play no part in this analysis. The ventral branchial structure of two stethacanthids, *F. falcatus* and *Stethacanthus* sp. 2, indicates that the primitive condition for the Chondrichthyes is to have two narrow basibranchials and posterolaterally directed ventral branchial elements with short, laterally or posterolaterally directed hypobranchials. As this condition also typifies Osteichthyes and can be supported for the Acanthodii, it can be hypothesized to be the primitive gnathostome condition (Nelson, 1968). The pharyngobranchial condition as well, consisting of simple, posteriorly directed pharyngobranchials lacking calcified interconnections, also supports Nelson's hypothesis of primitive design. There is also evidence for anterodorsally directed suprapharyngobranchial ligaments inserting upon the basicranium of *F. falcatus* (Lund, 1985).

The hyoid arch, unlike the branchial arches, is not primitive. The hyomandibula articulates on the postorbital process mesial to the palatoquadrate articulation, with little or no room for a spiracle (figs. 1, 5; Jarvik, 1977; Lund, 1985, in press). The suspensorium of the symmoriids appears to be the same as that of the stethacanthids, rather than aphe-tohyoidean, as stated by Zangerl and Williams (1975). Hypohyals have not been found.

The question of bone, and bones, in sharks, once clearly stated as absent, is no longer as straightforward. Bone tissue lacking cells has been identified in the bases of scales, teeth, and vertebrae of both modern and fossil chondrichthyans (Reif, 1979b; Orvig, 1966) and is found in the teeth of Stethacanthidae as well. However, the first dorsal spine and fin, the sclerotics, and distal clasper elements are apparently composed of bone in the Stethacanthidae. The capacity to produce acellular bone has not been lost in the Chondrichthyes; the production of cellular bone, however, has only been cited for one chondrichthyan by Zangerl (1968) and has been

called mesodentine by Orvig (1966). Two uniquely derived characters define the Chondrichthyes as presently understood: prismatic calcified cartilage and internal fertilization with copulation by copulatory organs derived from posterior extensions of the pelvic endoskeleton of males.

SYNAPOMORPHY SCHEME

A hypothesis of synapomorphies for the Stethacanthidae is summarized below (see fig. 11).

1. Coronodont tooth.
2. Tooth base lacking lingual plate.
3. Expanded bony lingual plate with interdental ligaments.
Loss of terminal membrane enameloid.
4. *Diplodus* tooth crown, basal plate with single tubercle.
One segmentally supported dorsal fin.
5. *Cladodus* tooth crown, basal plate with two tubercles.
Two segmentally supported dorsal fins.
Loss of anal fin.
6. Insufficient data.
Complete squamation (primitive).
7. Dorsal spine unornamented, outer dental layers lost.
Dorsal spine not present in all individuals.
8. Dorsal spine sagittally expanded into triangle.
Abbreviated heterocercal tail.
9. Lateral-line ring scales.
Pectoral metapterygial axis extended into "whip."
Dorsal spine and fin lost or a secondary sexual character.
Dorsal spine, where present, with an anteroventral shoulder.
Dorsal fin stenobasal where present.
Squamation reduced or absent, under secondary sexual control.
10. Greater than one pelvic metapterygial segment.
S curve in pelvic plate-metapterygial axis.
11. Single pelvic metapterygial segment.
First dorsal fin of males sagittally compressed.
12. Broadly rounded to subtriangular pelvic plate.
Greater than 14 pelvic radials.
13. Large pelvic diazonal foramina.
Dorsal spine apex posterodorsally oriented.
14. First dorsal fin approximates an equilateral triangle.
Dorsal spine apex vertically oriented.
15. Unresolved trichotomy.
Pelvic metapterygial axis fused or condensed.
Loss of secondary sexual dorsal and squamation characters.
- 15'. Parallel loss of first dorsal spine, fin.
Parallel loss of squamation.
Parallel development of rounded pelvic plate.
Parallel development of S-shaped metapterygium.
Parallel development of high pelvic radial numbers.
16. Dorsal spine apex forwardly oriented.
First dorsal fin either a rod, absent, or fused to spine.
Homocercal tail.
Calcified vertebral arcualia.
Clasper axis of five to six segments.
17. Dorsal spine apex oriented from 45° to 15° from horizontal.
First dorsal fin a rod.
18. Dorsal spine apex oriented horizontally.
Early spine development and growth.
First dorsal fin absent or fused to spine.
Pelvic metapterygium supports 60 percent of flat, unjointed radials.
Pelvic metapterygium triangular.
19. Dorsal fin a narrow acute triangle.
Dorsal spine apex vertical.
Inline pelvic plate metapterygial axis.
Pelvic metapterygium supports 60 percent of radials.
Clasper axis of 10 segments.
Squamation complete in males.

CONCLUSIONS

The Stethacanthidae are cladodont elasmobranchs characterized by several sexually dimorphic features. The unique first dorsal spine, fin, and surmounted squamation, accompanied by dorsal cranial squamation, oc-

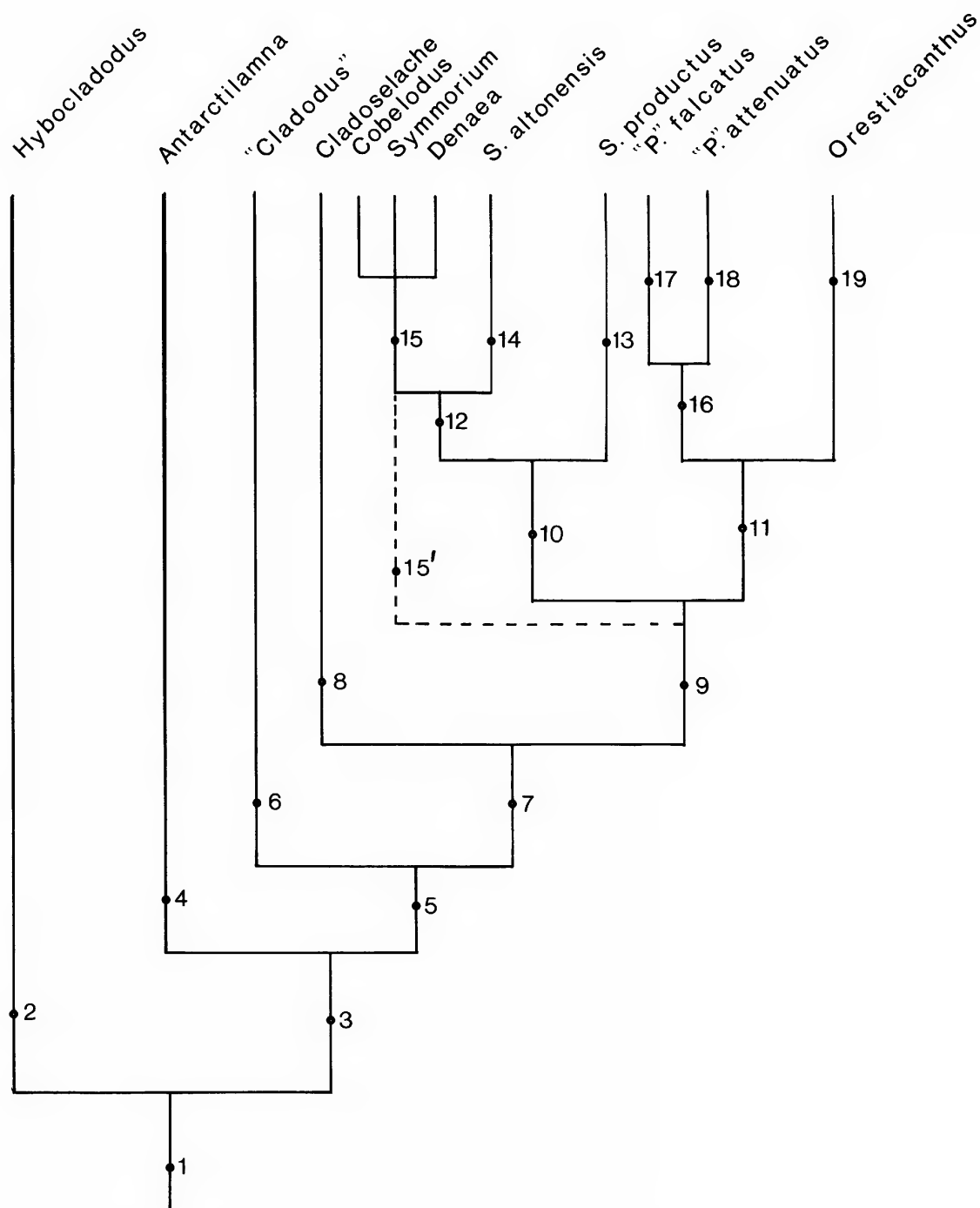


FIG. 11. Cladogram of the Stethacanthidae. See text for explanation.

cur only in mature males; other squamation also seems to be sexually determined. Branchial arches, where known, are sympleisio-

morphous at the gnathostome level. Acellular bone comprises several structures.

There are ample numbers of characters

permitting interspecific discrimination among the Stethacanthidae. At the present level of knowledge, however, few characters are consistently available that may be used in an analysis of suprafamilial interrelationships. Among these, braincase, squamation, first dorsal fin and spine data, and caudal structure fall into the category of potentially useful but sporadically available information. Continuously variable data, such as counts and measures, provide little insight. Pelvic girdles and fins provide the most readily available information on suprafamilial interrelationships. The pelvic girdles of the "Symmoriidae" are represented as being essentially identical to each other (Zangerl, 1981, figs. 76, 77, 80) as well as to those of *S. altonensis* (Zangerl, 1981, fig. 81, but compare this paper, fig. 7). The near identity of these girdles calls into question whether discriminative powers of the X-rays were insufficient to reveal fine morphology or whether the girdles are, in fact, all but identical (Zangerl, 1981; Zangerl and Case, 1976). Precisely the same questions can be raised about the nearly identical morphology of the braincases, jaws, and axial skeletons of the three purported species. The assumption that, as Zangerl (1981) has stated, it is indeed not possible to discriminate among the postcranial skeletons of the three species leads to several interesting consequences. The first is that generic-level separation of the symmoriids has not been proven, the species being recognizable only by proportional and numerical differences. Because a separate derivation of the Symmoriidae and Stethacanthidae would require numerous parallelisms (fig. 11, point 15'), all morphological data suggest that the "Symmoriidae" are derivable most parsimoniously as a sister taxon of *S. altonensis* among the Stethacanthidae. Consequently, a generic-level separation of *S. altonensis* and *S. productus* becomes a virtual necessity. The taxonomic structure of the group thus either must be expanded to a suprafamilial level, or the family Symmoriidae must be considered a *nomen nudum*, or both. The discontinuous variation of pelvic structures within the Stethacanthidae, ranging from plesiomorphous for the class to selachian level (Schaeffer and Williams, 1977; Young, 1982) and discontinuous variation in caudal structures

from low angle heterocercal to homocercal (Lund, 1984, 1985, in press) reinforce the potential taxonomic diversity of the Stethacanthidae.

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